PTYCHODUS PREDATION UPON A CRETACEOUS *INOCERAMUS*

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ABSTRACT. The type specimen of *Inoceramus tenuis* Mantell displays probable tooth impressions of *Ptychodus* on the ventral margin of the left valve. The predation is interpreted, and the general problem of vertebrate predation on Inoceramidae, which were the dominant Cretaceous bivalves, is discussed.

BIVALVES of the families Inoceramidae and Ostreidae dominate the epifaunal benthos of many non-Tethyan Cretaceous assemblages and are an important element of nearly all of them (e.g. Kauffman 1967, 1969). As such they should have been a primary food source for a variety of contemporary shell-feeding vertebrates: skates, rays, pycnodonts, shell-crushing sharks like *Ptychodus*, and reptiles like the mosasaurian *Globidens*.

Most Cretaceous ostreids were cemented epizoans with thickened, hard calcitic shells. They primarily attached to hard substrates which were difficult feeding areas for predatory vertebrates adapted to sifting softer sediments in search of bivalves, echinoids, and similar food. Thus, the Inoceramidae, epifaunal echinoderms, and various infaunal organisms were probably their principal prey. This is consistent with the inferred range of inoceramid adaptations and habitats, which were primarily related to unconsolidated and semiconsolidated substrates, with or without weak byssal attachment (Kauffman 1965, 1968, 1969).

Surprisingly, no definite cases of marine vertebrate predation on Inoceramidae have been previously documented. The impression that such predation was an important factor in the ecology and fossil preservation of inoceramids is purely circumstantial—selective marginal shell fragmentation and highly broken shell beds in quiet water deposits, marginal fragmentation of bivalved (living?) shells, common association of *Ptychodus* teeth with highly fragmented inoceramid assemblages, and common healed shell injuries which resemble the impressions of blunt teeth. This will be subsequently discussed. The discovery of two parallel rows of blunt tooth impressions along the ventral margin of the type of *Inoceramus tenuis*, with spacing and size characteristics closely matching those of known jaw assemblages of the contemporaneous shell crushing shark, *Ptychodus*, is the first good evidence for vertebrate predation on *Inoceramus* and is described below.

PTYCHODUS PREDATION IN *INOCERAMUS TENUIS*

Inoceramus tenuis Mantell occurs sparsely through chalks and marls of the Lower Cenomanian *Hypoturrilites carcitanensis* Zone and extends upward into the Middle Cenomanian *Turrilites costatus* Zone of Kennedy (1969). The type is from the Chalk Marl at Hamsey, Sussex (Woods 1911, p. 271, figs. 31, 32: Pl. 81, figs. 1*a*, *b* herein). These are all levels where fragmentation of *Inoceramus* shells (primarily within the *Inoceramus* ? *crippsi* lineage) is common. The holotype (Pl. 81, fig. 1*a*, *b*) is completely

uncrushed except for a series of moderately deep, subrounded, subequally spaced indentations—circular zones of crushing which do not perforate the shell—extending in two parallel rows across the mid-ventral and postero-ventral margins of the left valve (Pl. 81, fig. 1a, left lateral view; fig. 1b, diagonal left lateral view). The innermost row of three indentations is the best-developed. It is situated 10 to 20 mm in from the commissure, with tooth impressions 15–17 mm in diameter, and their centres 16 and 17 mm apart (measurements taken left to right along axis of row, Pl. 81, fig. 1b). The central impression is very slightly offset toward the ventral margin of the shell from the axis of the row (defined by terminal impressions). At least two very shallow, somewhat more irregular impressions lie in a second row marginal to the first, one each below and slightly offset to the right of the middle and right-hand impressions of the main row (as viewed in Pl. 81, fig. 1b). These have diameters of 13 and 15 mm respectively; the distance between them is 18 mm. Significantly, the margin of the left valve is broken off just below the zone of tooth impressions, including the area where additional impressions of the second (marginal) row would be expected to occur (left side of row, fig. 1b), and nowhere else on the shell.

The shape, size, and subregular arrangement of the impressions indicate a single bite by a vertebrate predator with rounded, elevated tooth crests which were closely spaced but not in contact. The teeth occurred in parallel rows (trending left to right in Pl. 81, fig. 1b) but adjacent teeth were moderately offset from one row to the next; some within each row were slightly out of line.

The impressions were made by teeth near or at the lateral edge of a jaw apparatus. Evidence for this is the lack of impressions nearer the centre of the shell, orientation of the rows of teeth (anterior–posterior trending) impressions *parallel to* the ventral margin of the *Inoceramus* shell, and curvature of the main row slightly concave toward the centre of the shell, ruling out the possibility that this row of teeth was situated at the anterior (convex outward) edge of the predator's jaw. This set of characteristics rules out normal skates and rays, which have smaller and generally flatter interlocking pavement teeth. It also eliminates reptiles like *Globidens* from contention, the teeth of which are larger, more widely spaced, and would have done much greater damage to the shell. Cretaceous pycnodont fishes had small mouths filled with very small, low, rounded, pebble-like teeth probably adapted for coral and algae 'grazing' on hard substrates (Romer 1955, p. 99). These do not compare with the observed tooth marks. Most Teleost fish have pointed teeth which are more close-set, and would have punctured the shell on contact, leaving small, close-set perforations.

Described Cretaceous *Ptychodus*, especially forms like *P. decurrens* Agassiz (Woodward 1911, pl. 51, fig. 4), possess all of the criteria defined above for the predator. Their teeth are knob-like, blunt, and moderately elevated on stout bases, with crests closely spaced but not in contact. The teeth are arranged in closely spaced parallel rows (anterior to posterior) with adjacent teeth in alternate rows slightly offset. Along lateral marginal

Fig. 1a, b. Lateral and oblique ventrolateral views, respectively, × 1, left valve of *Inoceramus tenuis* Mantell; holotype, BMNH 5890, showing probable *Ptychodus* tooth impressions in two parallel rows (axes left to right as oriented) and broken edge of ventral margin caused by single bite. Mantell Collection, from Cenomanian Chalk Marl of Hamsey, Sussex.
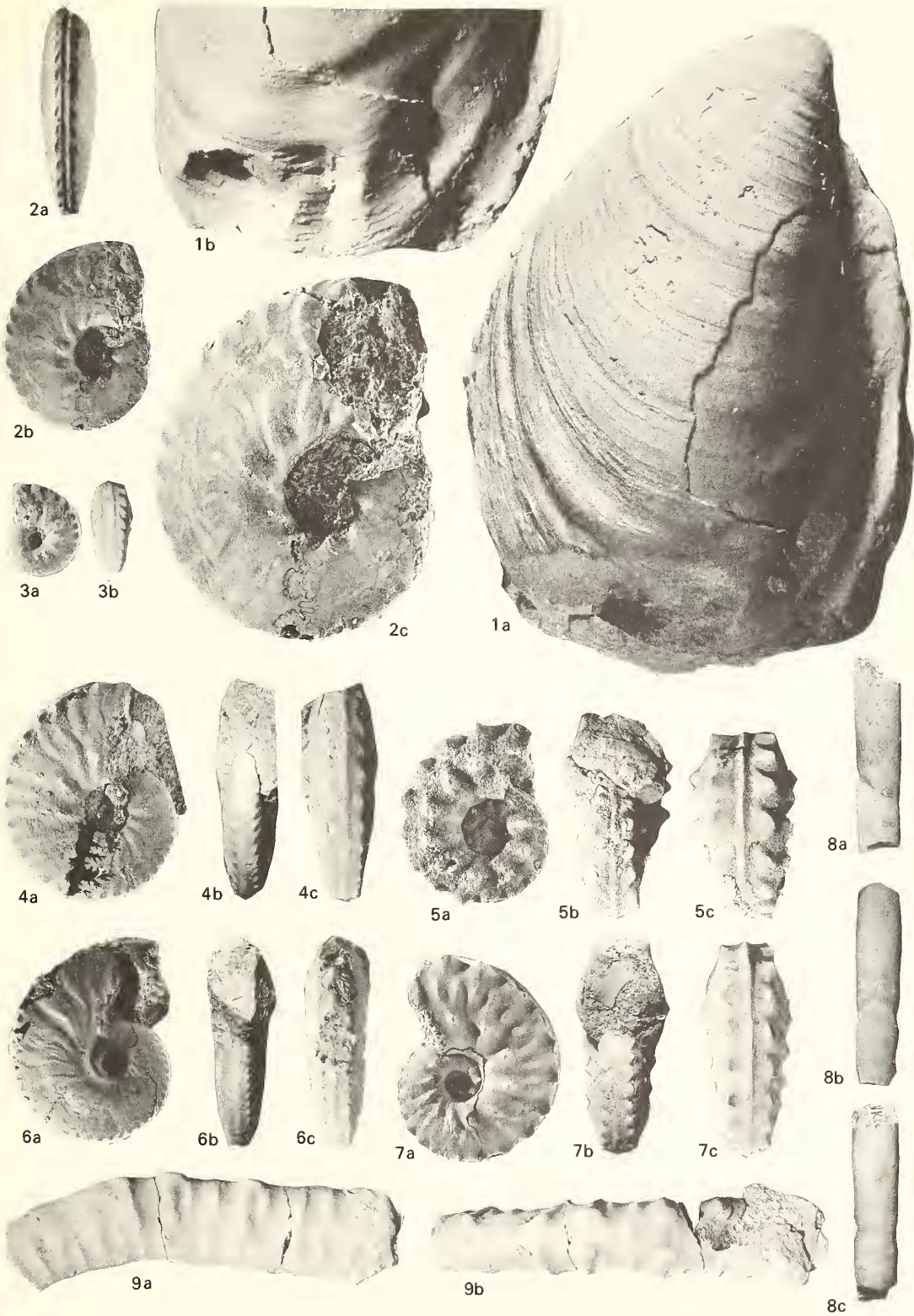
and submarginal rows, individual teeth within each row may also be slightly offset from the axis of the row. Woodward (1911, pl. 51) shows typical examples. Significantly, the spacing between tooth crests and rows and the diameters of individual tooth crests in jaw assemblages of *Ptychodus decurrens* Agassiz illustrated by Woodward from the English Chalk (1911, pl. 51, fig. 4) closely match the size and spacing of tooth impressions in *Inoceramus tenuis*.

I conclude from these data that the tooth marks along the ventral margin of *I. tenuis* are probably those from the lateral margin of a *Ptychodus* jaw, conspecific with or closely related to *P. decurrens*. The two species coexisted: *Inoceramus tenuis* has a Lower to Middle Cenomanian range; *Ptychodus decurrens* occurs sparsely in the Lower Cenomanian (Dibley 1912; Kennedy 1969) and more commonly in Middle Cenomanian to Turonian zones of the English Cretaceous sequence (Woodward 1911; Dibley 1912; Kennedy 1969).

An interesting problem connected with these observations is the absence of comparable tooth impressions on the smaller right valve of the type of *I. tenuis*. It is nearly complete, with only small pieces of the margin broken, and uncrushed (Woods 1911, fig. 32). From this, the orientation of the shell and predator at the time of attack can be determined, and is compatible with the implied life habits of both.

Weak pedalbyssal musculature and a thin, sinuous dorsoanterior byssal slit in *Inoceramus tenuis* indicate that it lived weakly attached to the substrate by a narrow row of byssal threads, with the dorsoanterior margin close to the bottom. *Inoceramus tenuis* is moderately inequivalve, with the left valve larger, considerably more inflated, and with the umbo projecting well beyond that of the right valve (Woods 1911, fig. 31). This further infers that in life the shell lay primarily on the dorsal and anterior flanks of the left valve, with the anterior flank and umbone held close to the substrate by byssal threads or even partially buried, but with the commissural plane of the shell inclined upwards and tilted so that the inhalent and exhalent areas of the mantle margin were elevated well above the sediment–water interface. In this position, with the valves gaping moderately (as now preserved; Woods 1911, fig. 31), the ventral margin of the left valve projected outward, beyond the more elevated margins of the gaping right valve by more than 20 mm (measured in the plane of the substrate surface; as reconstructed from the type specimen). The inferred orientation can be reproduced by orienting Woods's anterior view of *I. tenuis* (1911, fig. 31) so that the ventral surface of the umbo on the left valve lies tangential to a horizontal plane representing the substrate surface.

A predatory fish, like *Ptychodus*, feeding in characteristic fashion close and parallel to the bottom (or even slightly immersed in soft substrate) would first encounter the projecting left valve margin of the gaping shell if approaching the vulnerable feeding (ventral) edge. Distribution of tooth marks on the shell infer such an approach, but from a ventrolateral direction so that only the side of the fish jaw apparatus closed on the projecting left valve margin. Impression of tooth marks on only the ventral edge of the left valve indicates that the shell remained partially gaping during the attack. Failure of the animal to close the valves at or before predator contact, bringing the right valve within range of the teeth, may indicate that the bivalve was sick or recently dead from other causes. Most epifaunal bivalves have excellent sensory perception at the mantle margins and close the valves well in advance of near approach or contact by a large fish (or divers). Further, the *Ptychodus* made only a single bite, and then abandoned the

Inoceramus. This may further indicate a dead or dying organism. There is no evidence for subsequent healing of shell fractures caused by the bite. Burial was prior to complete organic decay, however, as the ligament remained intact long enough to keep the valves together until they were covered, and the crushed marginal shell areas did not fragment and disseminate. Broken shell pieces were probably held in place by bands of mantle muscles associated with, and inside of, the pallial line; the mantle tissue was presumably still in place at the time of the attack.

INDIRECT EVIDENCE FOR VERTEBRATE PREDATION IN INOCERAMIDAE

Although the preceding example is the first good evidence for vertebrate predation in Inoceramidae, a number of other observations strongly suggest that this was a widespread and ecologically important phenomenon. This largely indirect evidence, discussed below, has led a number of workers to propose limited to extensive vertebrate predation on these and other bivalves during the Cretaceous. Frey (1972, in press) and D. E. Hattin (personal communication) have suggested that fragmentation of *Inoceramus cuvieri* Sowerby in the Fairport Member of the Carlile Shale (Turonian; chalky limestone and shaly chalk facies), and of *I? deformis* Meek, *Volviceramus grandis* (Conrad), and *Platyceramus platinus* (Logan) in chalks, limestones, and chalky to calcareous clay shales of the Niobrara Group (Coniacian–Earliest Campanian), Western Interior United States, may well have been caused by vertebrate predation, especially by the commonly associated *Ptychodus*. These are all moderately deep- and quiet-water facies (Kauffman 1967, 1969). Speden (1971, pp. 56–60) has documented numerous occurrences of *Inoceramus* prism and shell fragment aggregations in the Albian-Cenomanian? Clarence Series of New Zealand which he interprets as disgorged material and fecal pellets from vertebrate predators. These occur in particular zones, usually between beds which bear whole to non-selectively fragmented or concentrated *Inoceramus* material. Of special interest is the scarcity of fragments from the thickened hinge areas of inoceramids in these regurgitated and fecal concentrations, possibly inferring that the predator selectively bit off the thin-walled part of the shell containing most of the animal.

Additional observations which suggest widespread vertebrate predation on Inoceramidae are as follows:

1. In Cretaceous strata which physically suggest very quiet-water depositional environments by their fine grain size, undisturbed thin bedding, and great lateral persistence of individual laminae, Inoceramidae up to several feet in diameter are often selectively crushed and fragmented around the ventral and ventrolateral margins. This is an area where the shell is thinnest and which is preferentially attacked by a variety of predators on living epifaunal and semi-infaunal bivalves. In some cases entire *Inoceramus* 'beds' are highly fragmented into angular pieces of various size, forming thin local calcarenites and coquinas in evenly and thinly bedded carbonates and clay shales which lack evidence of significant current scour or wave action. These fragmented and crushed shells are particularly common in the Fairport, Niobrara, and Austin chalks and shaly chalks, in the Blue Hill and Pierre dark gray shales of the United States Cretaceous, and in parts of the English, Irish, French, Danish, and German chalk sequences.

Where shells show only marginal fracturing it commonly extends to areas within the